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Decomposition of Coniferous Leaf Litter

C. S. Millar

Forestry Department
University of Aberdeen
Aberdeen
Scotland

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I. Nature of Coniferous Litter

Conifer leaves vary considerably in shape: from needles, found typically in *Pinus*, *Abies* and *Picea*, through the flattened minute leaves in *Cupressus*, *Thuja* and *Chamaecyparis* to the simple angiosperm-like leaves found in some species of *Podocarpus*. In most groups the leaves can be retained on the tree for more than one year but *Larix* and *Metasequoia* are deciduous.

The leaves usually have a thick waxy cuticle which may be covered with tubules. The cuticular waxes are complex chemically and vary both within and between species. They comprise mainly paraffin, ester and alcohol-soluble fractions containing high carbon components such as nonacosane and octacosanol (Schuck, 1969). The waxes are continuous over the stomata where they form an interlaced mat of tubules which influence gaseous exchange (Jeffree *et al.*, 1971) and must prevent the direct entry of larger fungal spores. These waxes are almost certainly weathered away during the

life of the leaf which may lead to a reduction in the resistance of older leaves to fungal pathogens. The waxes and cuticle also penetrate between and in some cases beneath the single layer of epidermal cells (Grahle, 1933). These regular, elongate cells typically have a thick cellulose wall and a small lumen. The lumen is connected by pores to neighbouring cells and these pores might provide pathways along which fungal hyphae grow within the leaf. The hypodermis, which is one or more cells thick, consists of smaller cells with a proportionately lower cellulose content.

The mesophyll cells are irregular in shape. When alive they have a high carbohydrate content and the walls may be lignified in parts. Within the mesophyll are resin canals which vary considerably in number both within and between species. The canals are composed of two concentric rings of cells. The resin produced by the inner cells is of importance as an antibiotic when needles are punctured by feeding insects such as aphids. Punctures which are sealed by resin exudation are rarely colonized by fungi whereas larger wounds, for example those caused by sawflies, cannot be sealed completely by resin and are invariably colonized by fungi. The endodermis is also partially lignified and may contain a casparian strip. It encloses a stele containing xylem and phloem surrounded by transfusion tissue.

The most recent detailed account of the anatomy of coniferous leaves is that of Napp-Zinn (1966).

The chemical composition of leaves is primarily a characteristic of the species but varies considerably with the age of the leaf and the time of the year. Tamm (1955) has studied the seasonal variation of a number of inorganic ions in *Pinus sylvestris* L. (Scots pine) and *Picea abies* (L.) Karst. Nutrients were stored in the needles in spring and translocated away in summer when the tree was growing actively. Nutrient content was most stable in autumn.

The chief inorganic components of needles are calcium, silicon, aluminium, potassium and phosphorus. Iron and sodium are present in relatively small amounts. The ash content is of the order of 1–6% of the oven-dry weight of fresh needles at needle fall. Calcium and silicon can together make up half the ash with silicon being particularly high in *P. abies* (Manakov, 1962). Owen (1954) has summarized some of the work on the inorganic content of needles. He found that only *Thuja occidentalis* L. and *Juniperus virginiana* L. of the northern coniferous forests have leaf calcium contents as high as hardwoods (over 2% oven-dry weight). A second group which includes *Picea abies* has 1–2%; but many species, including *Picea sitchensis* (Bong.) Carr, all the pines and *Tsuga canadensis* (L.) Carr, have less than 1% leaf calcium. Daubenmire (1953) gave data for 11 conifer species from North America.

The nitrogen content of living needles is of the order of 1–2% and has been shown recently, in *Pinus radiata* Don, to be related to the content of organic sulphur (Kelly and Lambert, 1972). According to these authors, there is no accumulation of nitrogen over that required to balance organic sulphur, so that protein formation is limited by the availability of sulphur. Kaludin and Kaludin (1968) studied the nitrogen content of *Pinus sylvestris* needles of different ages, and from trees from 10 to 70 years old. They found significantly more nitrogen in one-year-old needles as compared with two- or three-year-old needles and values were highest in 30–40-year-old trees.

Needles contain, as structural components, hemicelluloses, cellulose, lignin and closely associated substances, and proteins. In fresh needles of *Pinus* and *Picea* cellulose and lignin each account for about 20% of the dry weight, hemicellulose about 12% and crude protein only 1–5% (Mikola, 1954). Kaludin and Kaludin (1968) detected 21 amino acids by paper chromatography and Muir *et al.* (1964) identified 17 amino acids from *Pinus* needles. The organic acids, of which shikimic and citric appear to be most abundant, have been examined by Muir *et al.* (1964) and Bruckert (1970) in connection with studies on the movement of iron during litter decomposition. Terpenes are found in conifer leaves and may be of taxonomic value (von Rudloff, 1972).

Tamm (1955) has shown that there is a decrease in the nitrogen, phosphorus and potassium (NPK) content of needles towards autumn and, according to Manakov (1962) total NPK is less than 1% at needle-fall in some Russian pine and spruce forests.

Substances are washed from needles by rain. Tamm (1951) showed a large increase in the Ca, K, Na and P content of rain water collected under *Pinus sylvestris* trees as compared with that collected in the open, and several workers have shown that polyphenols can be washed from needles (Shepley, 1965). These polyphenols, which include cinnamic acid and flavenoids, are perhaps the most important substances in needles in relation to decomposition. The protein-tanning theory of litter decomposition suggests that polyphenols form complexes with the proteins of the needle mesophyll cells immediately before leaf fall. The complexes show considerable resistance to microbial decay so that, in mor litter, mesophyll cell fragments can still be detected in the humus layer (Handley, 1954).

II. Pattern and Amount of Leaf Fall

The total amount of plant organic matter in a coniferous forest on a well-drained site might be of the order of 300 t ha^{-1} dry wt depending upon the species and age of the crop, the site and many other factors. The weight

of foliage on the trees in a mature temperate evergreen coniferous forest is of the order of 2–24 t ha^{-1} (Ovington, 1965; Metz, 1954).

Needle retention varies both within and between the species but total annual needle fall is of the order of 1–5 t ha^{-1} and accounts for 60–80% of the total litter fall. Bray and Gorham (1964) concluded, from their survey of the data on litter production, that gymnosperms produce about one-sixth or 0·5 t ha^{-1} year more litter than angiosperms. The total litter containing recognizable plant remains varies within very wide limits and may reach 400 t ha^{-1} in stands where there is accumulation of peat.

Reviews relating to litter production are to be found in the papers by Alway and Zon (1930), Chandler (1943), Kittredge (1948), Owen (1954), Bray and Gorham (1964), Ovington (1965) and Rodin and Bazilevich (1967).

The factors affecting litter fall have been considered in detail by Bray and Gorham (1964). Generally, litter production is greater the warmer the climate, the lowest values of less than 1 t ha^{-1} year being obtained from the U.S.S.R. (67°N 37°E) and Norway (62°N 10°E) and the highest values from Japan (35°N 135°W), California, U.S.A. (35°N 82°W) and New Zealand (38°S 176°W). Chandler (1943) found a range of annual litter fall from 10 species in north-east America of 2·7–4·4 t ha^{-1}. In the Pacific North West, Tarrant *et al.* (1951) found from 0·3 to 2·5 t ha^{-1} year. Although litter production appears to decrease with increase in altitude, the effects are confounded by changes in soil moisture conditions (Ebermayer, 1876).

As site quality increases, so also does litter production (Bonnevie-Svendsen and Gjems, 1957). In closed canopy forests litter production is affected little by tree density but thinning results in at least a temporary reduction in litter production. The age of the stand appears to have little effect on litter production once the canopy has closed but long-term studies on this point are lacking. Deliberate removal of undecomposed litter reduces tree growth.

Among the gymnosperms, the pattern of deposition of leaf litter varies from distinctly seasonal as in *Pinus sylvestris* to non-seasonal as in *Picea abies* in Europe. Some species such as *Picea sitchensis* in Britain and *Cryptomeria japonica* (L.f.) D. Don in Japan show a tendency towards a bimodal spring and autumn pattern of needle fall (Bray and Gorham, 1964). In north-east America the greatest needle fall occurs, along with leaf fall in the deciduous broad-leaved trees in October–November (Chandler, 1943) whereas in New Zealand some exotic pines tend to drop their needles mainly in the autumn (March to May) whilst the native broadleaved *Nothofagus* is deciduous in spring (October–November) (Will, 1959).

Annual variation in litter production is considerable. Occasionally, the

ratio of the maximum to minimum annual total litter production may reach 5 but more normal ratios are 1·5–3·0. Annual variation is related not only to needle production but also to flowering and seed production. Severe environmental factors such as drought and storms can affect needle fall and needle pathogens can have the effect of either increasing or reducing the weight of the annual fall of needles, depending upon the timing and the nature of the attack.

A considerable amount of energy is stored in the litter. In a *Pinus sylvestris* stand, Ovington (1961) estimated that needle production is about one-third of total tree production over the life of the stand. The calorific value for the attached needles and the freshly fallen needles was about 5000 cal g^{-1} of oven-dry matter but decreased with increase in depth in the litter to about 3500 cal g^{-1} in the humus layer. Thus the energy already released by decomposition of the needles by the microflora and meiofauna in a 55-year-old stand of *Pinus sylvestris* was about 9000×10^8 cal ha^{-1}. The energy still contained in the existing needle litter amounted to about 600×10^8 cal ha^{-1}.

III. Stages of Decay

The decomposition of coniferous leaves results most often in the formation of a mor type of soil characterized by an accumulation of raw humus with a low base status and a low pH. In certain circumstances, the details of which are not fully understood, a mull type of soil may be formed. Such soils are most likely to be formed on sites with a relatively high base status and a resident population of *Lumbricus* (Wittich, 1963). A detailed discussion of mull and mor formation in relation to forest soils was presented by Handley (1954). The present account is mainly concerned with the decomposition of coniferous leaf litter under mor conditions.

Although the decay process is more or less continuous, it is convenient to recognize stages in this process. The A horizon may be divided thus:

$A_{000}L$	freshly fallen, undecomposed needles.
A_{00} F_1	dark brown intact, recognizable needles extensively colonized by fungi.
F_2	greyish, fragmented, compressed but recognizable needles containing hyphal fragments and animal faeces. Mesophyll collapsed.
A_0 H	humus-like amorphous mass of animal faeces and needle and microbial fragments.
A_1	an intimate mixture of humus and mineral soil.

These stages have been decribed mainly for *Pinus* but are recognizable also beneath other genera such as *Picea* and *Abies* (Hayes, 1965*a*, *d*; Brandsberg, 1969). Obviously, needles which are infected whilst still attached to the tree will join the litter, perhaps prematurely, in a more or less decayed state. Little work has been done on this aspect of decomposition, but Gremmen (1957) recognized that the colonization of naturally fallen needles and of needles shed after infection by parasites such as *Lophoderium pinastri* was quite distinct from colonization of needles of felled trees. He recognized in particular a *Sclerophoma* stage in which grey, dry needles, attached to damaged shoots on the tree, were colonized by *Sclerophoma pithyophila* and *Cenangium acuum.*

Work at Aberdeen has shown that needle pathogens such as *Lophodermella sulcigena* are active in decomposing the mesophyll tissue of attached needles whilst secondary organisms such as *Hendersonia acicola* can remove, more or less completely, the cellulose content of the needle reducing it to a skeleton of epidermal waxes and lignified tissues (Millar and Williamson, unpublished data).

In a healthy stand the L layer will contain more or less undecomposed needles on the surface. Under mor conditions the cell contents are decomposed rapidly in the L layer and the epidermal and hypodermal cell walls in the F layers. Handley (1954) showed that in *Picea abies* and *Abies pinsapo* Boiss. the vascular tissue of the needles disappeared rapidly leaving a residue of leaf mesophyll tissue which contained stabilized protein and was generally very resistant to microbial attack. By contrast, Meyer (1962) examined the decomposition of *Picea* needles in a brown earth by direct observation and using thin sections and found most rapid decay in those tissues with little lignification so that apparently complete needles were in fact hollow. In the F_1 layer the mesophyll was entirely decomposed.

Stark (1972) suggested that Basidiomycetes with dark hyphae growing on the surface of needles of *Pinus jeffreyi* Grev. and Balf. under snow were responsible for the removal of the needle cell contents and most of the nitrogen and phosphorus, during the first winter of decomposition in Nevada, U.S.A. Cellulose was decomposed mainly in the F layers.

Needles in the F_2 layer undergo comminution by a variety of mites and springtails, whilst decomposition by fungi, bacteria and Actinomycetes continues until the needles are reduced to humus. Although humus is described as amorphous, it often contains recognizable fragments of mesophyll and other cells.

The stages in the decay process have also been described in the work of Ward (1952), Kendrick (1958*a*), Will (1968) and Guittet (1967) for species of *Pinus* and by Jacot (1936, 1939) for species of *Abies* and *Picea*.

IV. Microfloral Succession

Most of the work on the microflora in relation to the decomposition of coniferous leaf litter has been on pine litter (Ward, 1952; Gremen, 1957; Kendrick, 1958*b*; Hayes 1965*b*; Tubaki and Saito, 1969; Brandsberg, 1969) with some comparison to other genera by Hayes (1965*a*, *d*) and Brandsberg (1969).

In general, the early colonizers of coniferous leaf litter are bacteria, Ascomycetes, Deuteromycetes (= Fungi Imperfecti), and some Basidiomycetes, which attack simple carbohydrates and cellulose. These are followed by Phycomycetes, particularly members of the Mucorales which can utilize the fungal breakdown products, perhaps in combination with the meiofauna.

The microfloral succession starts when the leaves are in the bud (see Pugh, Chapter 10). Bud scales are colonized by *Aureobasidium pullulans* and, at least in pines, by *Sclerophoma pithyophila*. If the growing needles are damaged by abrasion or by insects they are often colonized by *S. pityophila*. Various fungal pathogens and in particular Ascomycetes and rusts can infect vigorously growing needles and cause premature needle cast, either directly or by providing an entry-point for secondary organisms. *Lophodermella sulcigena* infects young *Pinus sylvestris* needles which are then further infected by *Hendersonia acicola* or *Lophodermium pinastri* and finally by *Naemacyclus niveus* which causes needle cast (Watson, 1971).

Needles which are green and appear to be healthy often contain a variety of fungi. In *Pinus nigra* var. *maritima* (Aiton) Melville, and *Pinus sylvestris* most needles are infected in their second year by *L. pinastri*, which remains in a quiescent state until the needle senesces. In addition, species of *Cephalosporium* and *Fusicoccum* might also be present (Millar, unpublished; Kendrick 1958*b*; Hayes 1965*b*). Fungi on living needles can be divided into three types; surface fungi which grow and sporulate only on the needle surface, e.g. *Coniosporium* sp., *Trimmatostroma* sp., *Aureobasidium pullulans*, and various yeasts; vigorous pathogens which can infect young and healthy needles, e.g. *Lophodermella sulcigena*, *Coleosporium senecionis*; weak pathogens, e.g. *Lophodermium pinastri*, *Sclerophoma pityophila*, which may enter the needle directly but remain in a quiescent state or which act as secondary invaders of tissue damaged previously by strong pathogens or insect pests. Thus, at needle fall, a variety of fungi may be present in or on the needles.

These early colonizers of living needles often induce a host reaction which prevents their spread to the base of the needle, thus delaying needle cast. The nature of this reaction has not been worked out.

The most detailed study of the succession of fungi on decomposing coniferous litter is that of Kendrick (1958*b*; and summarized by Kendrick,

1958*a*; Kendrick and Burges, 1962). He examined the litter in a stand of *Pinus sylvestris* at Delamere Forest, England, by a variety of techniques over 15 months from January to March. Although his techniques were chosen to study the dematiaceous fungi in particular, his results seem to give the clearest idea of the succession available to date since the effect of fast-growing fungi was minimized.

At needle fall the needles bore a reticulum of brown hyphae which was removed rapidly by the meiofauna once the needles entered the litter. At this time there was an increase of weak pathogens and surface fungi. During the 6 months or so spent in the L layer *Fusicoccum bacillare* and *Lophodermium pinastri* fruited and then declined in frequency. Meanwhile, *Desmazierella acicola* colonized the needles but it was not clear whether this fungus replaced the previous two or whether it invaded tissue not colonized previously.

In the F_1 layer *Aureobasidium pullulans* was replaced on the surface by the Hyphomycetes *Helicoma monospora* and *Sympodiella acicola* (Kendrick 1958*b*, *c*) and *D. acicola* dominated the internal tissues. *D. acicola* formed zones of black pigment within the tissues at the limits of its growth and produced conidiophores through the stomata. These conidiophores, together with those of the surface fungi, were grazed by ectophages such as mites, springtails and enchytraeid worms. Kendrick and Burges (1962) pointed out that at this stage adjoining sections of the same needle might be decomposed at different rates and by different combinations of microorganisms and that this situation persisted into the F_2 layer.

In the F_2 layer, which the needles entered in the third year after needle fall, the meiofauna assumed more importance. Ectophages continued to graze the fungal hyphae and conidiophores whilst endophages rapidly comminuted the needles which were attacked by *L. pinastri* and *D. acicola*. Needle fragments which escaped extensive internal attack accumulated in the F_2 layer and were colonized externally by *Trichoderma* and *Penicillium* and internally by Basidiomycetes and a sterile dematiaceous form. Needles were in this layer for about 7 years by which time the fungi and meiofauna had reduced them to an amorphous mass typical of the humus layer.

Kendrick did not study the humus layer but it seems clear from other work that species of *Mucor*, *Mortierella*, *Penicillium*, *Trichoderma* and *Chaetomium* are dominant at this stage (Ward, 1952; Brandsberg, 1969). Indraratne (1964) found *Trichoderma viride*, *Penicillium decumbens*, *Mortierella alpina* and *Cylindrocarpon radicicola* to be prevalent in the humus layer and also in the C horizon.

In addition, Actinomycetes were active in the F_2 and humus layers (see Goodfellow, Chapter 9). It is generally assumed that Actinomycetes and bacteria are intolerant of the acid conditions found in mor litter but recently

Williams *et al.* (1971) have demonstrated the existence of both neutrophilic and acidophilic Actinomycetes, in a pinewood soil in England, in numbers at least equalling the fungal propagules. At pH 3·5 in the F_2 and humus layers, over 2×10^6 propagules per gram of dry soil were found. Lloyd (1969) had suggested that Actinomycetes in soils were mainly conidial forms of Streptomycetes and that mycelium was associated with active growth, particularly in microsites containing organic matter. In 1971, Williams and Mayfield demonstrated that occasional periods of activity of the neutrophilic Streptomycetes occur in acid soils in microsites where ammonia, released by the fungi from chitin, was absorbed on organic fragments.

The role of bacteria in acid litter decomposition is not clear. Mikola and Hintikka (1957) found an overwhelming dominance of only a few species of bacteria in *Pinus sylvestris* litter in Finland and Stout (1961) in a survey of soils in New Zealand obtained counts varying from 10^4 g^{-1} wet wt in the L layer under *Pinus radiata* to 10^7 g^{-1} under *Agathis australis* (Lamb.) Steud. Species of *Flavobacterium* were common but might have been washed down from leaves. Species of *Bacillus*, *Pseudomonas* and *Achromobacter* were also present, especially in the humus layer. Most strains could use ammonia as a sole source of nitrogen and few strains could use nitrate.

In a similar study, Goodfellow *et al.* (1968) found about 6×10^5 bacteria per gram in the A layer at pH 3·6 and 9×10^5 in the C horizon at pH 8·6 under *Pinus nigra* var. *maritima* in England. Species of *Bacillus* predominated in the A_1 layer and Gram-negative rod types such as *Pseudomonas* spp and *Achromobacter* spp. in the C horizon. Although bacteria were isolated from the A_1 layer at pH 3·6 none grew on test plates at pH 4 and few at pH 5, suggesting that pockets of high pH occurred in the A_1 horizon. The bacteria were observed to be associated with organic particles, reinforcing the view that bacteria and Actinomycetes might occupy the same ecological niches in coniferous litter decomposition.

Few authors have mentioned Myxomycetes in their work on conifer litter. Ward (1952) recorded *Leocarpus fragilis*, *Physarum nucleatum* and *Trichia varia* in *Pinus* plantations in England but did not relate them to the decomposition process. Cavender (1972) found that members of the Acrasieae occurred frequently and abundantly in soils in boreal *Picea glauca* (Moench) Voss–*Abies balsamea* (L.) Mill. forests in North America. *Dictylostelium mucoroides* and *D. minutum* were common and there was some indication that large populations, of up to 20,000 clones g^{-1} litter wet wt, might be associated with areas of high bacterial densities.

In comparing work on the fungal decomposition of litter it must be emphasized that lists of species vary considerably according to the techniques used for collection of the material and its processing. In particular,

the time and storage conditions between collection and isolation or observation are critical. Incubation of unsterilized material in collection tubes or bags, even for 24 h, can allow surface fungi to colonize needle tissue and give false results when needles are subsequently surface sterilized and plated out on nutrient agar (Millar, unpublished).

Ward (1952) in the first detailed study of litter decomposition in pinewoods, conducted near Nottingham, England, listed about 120 different fungi. Of these, 44 were Basidiomycetes, recognized by direct observation, and 48 were Deuteromycetes obtained in pure culture. In addition, 13 Phycomycetes and 18 Ascomycetes were obtained. The most frequently isolated genera were *Trichoderma*, *Penicillium*, *Mortierella*, *Mucor* and *Aureobasidium*. Basidiomycetes were active in the L layer but decreased with increase in depth as did the pycnidium-producing Deuteromycetes and the Ascomycetes. There was no fundamental difference between the floras of needles from mixed Corsican and Scots pinewoods and pure Corsican pinewoods. Ward noted, but did not name, some species which were to be described later by Kendrick (1958*c*).

Hayes (1965*a*, *d*) studied the decay of litter of *Abies grandis* (Dougl.) Lindl., *Picea sitchensis* and *Pinus sylvestris* at a site in North Wales. He recognized six decay stages based on colour and texture of the needles and described a succession, similar to that described by Kendrick (1958*b*), which did not vary much between tree species. *Desmazierella acicola* was present on *Pinus* and *Picea* but not *Abies* litter and *Fusicoccum bacillare* fruited occasionally on living needles and thus occurred earlier in the succession than described previously.

Hayes (1965*b*) also studied the litter in a 70–80-year-old *Pinus sylvestris* wood at Rannoch in Scotland. His results differed considerably from those which he had obtained earlier in Wales, and from those of Ward (1952), Kendrick (1958*b*) and Gremmen (1957). At Rannoch about 120 species were isolated. The species most common on unsterilized needles were *Mucor hiemalis*, *Penicillium spinulosum*, *Graphium* sp. and *Trichoderma viride*. Surface sterilization removed mainly *Mucor* and *Mortierella* species. On new litter *Desmazierella acicola*, *Aureobasidium pullulans*, *Cephalosporium acremonium* and *Geotrichum candidum* were also relatively abundant. No clear succession emerged from this work.

Badurowa and Badura (1968) examined fallen needles of *Pinus sylvestris* by direct observation in moist chambers and found a predominance of members of the Moniliaceae and dematiaceous species.

Brandsberg (1969) pointed out that work on coniferous litter decomposition has been concentrated in Britain and the Netherlands and that in the U.S.A. only the mineral layers have been studied in detail. He made a qualitative study of the mycofloras involved in the degradation of litter of

Abies grandis, *Pinus monticola* Douglas and *Pinus ponderosa* Douglas ex.P. and C. Lawson in Idaho, U.S.A., but noted no pronounced differences between the three tree species. Dilution plates from homogenized needles yielded 128 species, predominantly Deuteromycetes. In the L layer *Aureobasidium* and *Cladosporium* were found and *Coniothyrium* sp. appeared to be an early colonizer. *Coniothyrium fuckelii* is isolated regularly from senescent and diseased Corsican pine needles in Scotland (Millar, unpublished). In Brandsberg's work, the F layer was characterized by species of *Penicillium* and the A_1 layer by Zygomycetes, Hyphomycetes and *Chaetomium* sp. Notable omissions from Brandberg's list are *Desmazierella acicola*, *Fusicoccum bacillare* and *Penicillium spinulosum* which are isolated regularly in Europe. An examination of the amorphous peat under *Picea mariana* (Mill.) BSP–*Larix laricina* (Du Roi) K. Koch and *Thuja occidentalis*–*Abies balsamea* in Wisconsin, U.S.A., showed species of *Penicillium* and *Mortierella* to be most prevalent (Christensen and Whittingham, 1965).

In Japan, Tubaki and Saito (1969) examined litter of *Pinus densiflora* Siebold and Zuccarini and found that three species, *Chaetopsina fulva*, *Endophragmia alternata* and *Desmazierella acicola*, were widespread and played a major part in the early decay of needles.

The work of Gremmen (1957, 1960) serves to emphasize the paucity of information on decomposition since few of the 19 species which he recorded on *Pinus* needles by direct observation have been included in the lists prepared by other workers using various isolation techniques.

Although studies on fungal succession in coniferous litter have tended to concentrate on the microfungi the role of the Basidiomycetes in decomposition should not be underestimated. Hora (1959) has drawn attention to the dearth of observations and experiments on the ecology of the higher fungi. The main obstacle has been an inability to recognize Basidiomycete species from their mycelium. This mycelium is often prolific in the L and F layers. Ward (1952) named 44 Basidiomycetes in two pinewoods and Richardson (1970) has estimated the total productivity in a *Pinus sylvestris* wood in Scotland to be a quarter to half a million sporophores per hectare per year, weighing up to 460 kg fresh or 30 kg dry. The majority of the sporophores were formed in the period from August to October.

Basidiomycetes in litter decompose cellulose and lignin and it is probably de-lignification that reduces the needles to a greyish colour in the F_2 layer (Mikola, 1958). Although some Basidiomycetes, such as *Marasmius androsaceous* and species of *Mycena*, colonize individual needles in the F_2 layer, most are active as a mycelial weft spreading through the litter. Recently, Gadgil and Gadgil (1971) have claimed that these wefts belong to mycorrhizal fungi and actually suppress litter decomposition. Their experimental results might, however, be explained in terms of water relations which were

apparently not monitored. Much more work is required on the role of Basidiomycetes in coniferous litter decomposition.

V. Microfaunal Succession

Mites (Acarina) and springtails (Collembola) cause considerable comminution of conifer leaves whilst feeding on fungi in the litter. Some enchytraeid worms are thought to feed on the faeces of Collembola. Fungi and bacteria may also be eaten by protozoans or nematodes so that whereas fungi are most active in the upper layers of litter the meiofauna is most active in the F_2 and humus layers.

Earthworms are not common in coniferous litter, which is usually of a mor type with a pH of less than 4·5, but where mull-forming conditions occur, conifer needles are recomposed rapidly once they have been removed from the litter surface to the wetter environment of worm burrows (Wittich, 1963). Cellulases and chitinases are present in the gut of lumbricid worms but it is not absolutely clear whether these are produced by the worms or by bacteria or protozoa present in the gut.

Enchytraeid worms are very abundant in podsols in northern coniferous forests (Abrahamsen, 1972) and are probably important in mixing debris with the mineral soil. Since ingested plant material does not change much on passing through the gut, it appears that these worms lack the enzymes necessary to degrade plant cell wall polysaccharides. O'Connor (1967) suggested that they feed mainly on Collembola droppings. Abrahamsen (1972) found *Cognettia sphagnetorum* to be dominant over 22 other species in most plots in *Pinus sylvestris* and *Picea abies* forests in Norway and attributed the variation in seasonal abundance and vertical distribution to soil-moisture changes.

Nematodes are also common in coniferous litter (Ward, 1952; Nef, 1957). They feed on living protoplasm of fungi, bacteria and Protozoa. They are known to produce chitinase and amylase but apparently have no ability to utilize cellulose. Nef (1957) estimated that there were 10^8 protozoans in each square metre of litter and Ward (1952) stated that they were present in "large numbers". Little specific work on their nutrition in soils under conifers has been recorded but it is assumed that they are predators, mainly on bacteria and possibly on fungi.

There seems to be little doubt from the literature that mites are one of the main agents in the decomposition of coniferous needle litter (see Harding and Stuttard, Chapter 15). They are primarily, if not exclusively, fungal feeders and even show preferences for certain fungi (Hartenstein, 1962). They eat fungal hyphae growing within needle tissue and also graze on fungal hyphae growing on the needle surface or protruding through stomata (Kendrick and Burges, 1962).

In general, intact, undecomposed needles contain no mites but eggs are laid in the needle, by ovipositing through the cuticle, and the mite larvae ingest fungal tissue, depositing faeces in the cavity produced by feeding. The larvae pass through several moults to the adult stage. The adult cuts a hole through the epidermis to emerge for mating and eggs are laid throughout the growing season (Jacot, 1939). Unfortunately, little is known about the metabolism of mites and the chemical changes brought about in their gut but the physical disintegration and comminution which they produce are undoubtedly important in decomposition. Faecal pellets, which are round or cylindrical, measure on average 5×3 μm and in the humus layer of a moder soil examined by Boswell (1956) practically all the organic matter was mite excrement.

The feeding behaviour of Phthiracarid mites of the Oribatidae have been studied in decomposing litter from *Abies grandis*, *Picea sitchensis* and *Pinus sylvestris* in Wales by Hayes (1965*c*). Three species *Haploderma magnum*, *Phthiracarus piger* and *Oribotritia loricata* were studied in detail and all showed a definite preference for feeding in the F layers, although *H. magnum* fed also on the leaf sheaths of freshly fallen litter. None of these three mites showed a preference for needles from a particular tree species and faecal pellets did not vary in appearance with change in food species. The mites did not feed at low relative humidity.

Usher (1971) studied the distribution of members of the Mesostigmata in a stand of *Pinus sylvestris* in Scotland. Twenty-two species or genera were recognized from the F layer, including *Olodiscus minimus*, *Paraxercon radiatus*, *Pergamasus lapponicus*, *Trachytes pyriformis* and *Veigaia nemor ensis*. A few species showed a seasonal distribution with only one maximum but most showed two or three maxima. Temperature controlled vertical distribution, the population size reducing with decrease in temperature at any one level in the litter.

Metz (1971) found that the vertical distribution of mites in the F layers of a stand of *Pinus taeda* L. was controlled largely by the moisture gradient in the litter. The mites moved between the organic layers and the mineral soil as moisture changed. A decrease in moisture resulted in a decrease in the mite population. In the stand studied by Metz, oribatid mites outnumbered the mesostigmatids by over 10:1.

Springtails are also very important agents in the decomposition of coniferous leaf litter since, whilst feeding on fungi, humus and faeces they promote comminution. Poole (1959) examined the gut contents of Collembola from a plantation of *Pseudotsuga menziesii* (Mirb.) Franco in Wales. He found that the larger species fed mainly on soil fungi whereas small species appeared to feed directly on the humus and on faeces in the litter. Some species such as *Amiridia granaria* were fluid feeders only but others

such as *Tanocerus longicorms* had gut contents comprising, in addition to fungal hyphae, tracheids, guard cells and mesophyll cells.

The Collembola feeding on fungi may show specificity for spores or hyphae. Farahat (1966) using Collembola extracted from an undefined soil found that *Entomobrya lanuginosa* fed on both hyphae and spores whilst *Isotomiella minor* fed only on spores.

Springtails are active mainly in the F layers. Usher (1970) found an average density of 38,250 Collembola per square metre in a *Pinus sylvestris* forest in Scotland. Twenty-four species, including *Friesia mirabilis*, *Onychiurus absoloni*, *Tullbergia callipygos*, *Folsomia quadrioculata* and *Isotoma sensibilis*, were present in the F layers only. The majority of these showed only one population peak each year but peaks occurred at different times for different species. Usher considered that temperature was the factor most important in causing vertical migration of Collembola but Stark (1972) found that Collembola were extremely abundant and active under snow in a stand of *Pinus jeffreyi* in Nevada, U.S.A.

Using radiotracers, Kowal and Crossley (1970) have shown that, in an artificial laboratory ecosystem composed of *Pinus echinata* Mill. litter, the micro-arthropods fed mainly in the L and F_1 layers. Among the Collembola the larger jumping forms (Entomobryomorpha) showed a definite preference for feeding in the L layer. Non-jumping forms (Poduromorpha) fed mainly in the lower layers, obtaining 39% of their food from the F_2 and 16% from the humus layer.

VI. Chemical Changes

There have been few detail studies specifically on the chemistry of the decomposition of coniferous leaf litter (see Gray and Williams, Chapter 19). Sokolov and Karpova (1965) studied decomposition, humification and mineralization in a mixed pine forest podsol. They found that the first substances decomposed were the water-soluble, alcohol and benzene extractives such as starch, hemicelluloses and amino acids. Inorganic residues and lignin were decomposed later. The remaining humus contained humic acid, fulvic acid, various hydrolysable residues and 7% of waxes and resins.

The enzymes (e.g. cellulase, xylanase and lignase) necessary for the breakdown of litter are not normally produced by soil invertebrates, except perhaps by protozoa, and the microflora are therefore responsible for primary decomposition. Mites and springtails in particular do not appear to possess carbohydrases. The action of the microflora is to break down complex polysaccharides into assimilable monosaccharides. In general, hemicelluloses and cellulose are broken down by Ascomycetes and Deuteromycetes, lignin by Hymenomycetes and Gasteromycetes and sugars and pentosans by Phycomycetes, especially Mucorales.

Autolytic processes in drying leaves lead very quickly to the decomposition of sugars, proteins and fats in fresh fallen leaves leaving compounds which are difficult to hydrolyse such as lignin, cellulose, terpenes and tannins.

It is a well known phenomenon that dead leaves release a variety of inorganic salts and organic substances when soaked in water. Typically, 1–3% of the dry weight of needles may be lost after soaking for one day. Nykvist (1963) obtained 1·1% organic and 0·3% inorganic leachates from whole *Picea abies* needles and 0·9% organic and 0·1% inorganic leachates from *Pinus sylvestris*. The leachates, from the same two tree species, which were examined by Muir *et al.* (1964) contained more than 10 amino acids, several sugars and various aliphatic acids. In non-sterile conditions most of these leachates had been decomposed by micro-organisms after only 4 days. As Nykvist (1959) stated, it is likely that these leachates influence the growth of soil fungi during the early stages of decomposition.

According to data compiled by Ovington (1965), litter fall and decomposition releases about 80% of the total minerals in the biomass of a stand, the remainder being retained in the living parts of the tree. As one would expect, most minerals tend to increase down the litter profile. The dissolution of elements such as Ca, K, Mg, Mn, Na, P, S and N from the litter exceeds their removal from the soil because they can be biologically or chemically fixed in the lower horizons (Smirnova and Sukhanova, 1964). Iron, aluminium and silicon have a special role in mor soil formation since they form complexes with the organic acids produced during litter decomposition which are recognized by the colours they impart to the B horizon (Manakov, 1962).

The sugars present in freshly fallen needles are decomposed rapidly, probably by bacteria. The first step in the degradation of insoluble cellulosic substrate to soluble sugars is by extracellular enzymes. Crystalline forms are converted by cellulases first to an intermediate soluble form and then to sugars (Selby, 1968). Invertase, which is active in the decomposition of these nitrogen-free compounds, decreases in activity with increase in depth. Although fungi are mainly responsible for the breakdown of cellulose and hemicelluloses in coniferous litter in some cases cellulose might be degraded by Actinomycetes (Goodfellow *et al.*, 1968).

Litter from *Pinus strobus* L. was examined over 1200 days for sugars by acid hydrolysis (Sowden and Ivarson, 1962). It was found to be high in arabinose and mannose, which remained more or less constant over the first 200 days. Galactose was constant over the test period whilst other sugars, such as rhamnose, ribose, xylose, glucose and fucose decreased slightly. It is known, from the work of Goodfellow *et al.* (1968), that bacteria from pine litter can attack these sugars.

The chemical structure of lignin is not yet clearly understood. It has a high molecular weight, a low solubility, and it contains large amounts of carbon (62–69%) relative to cellulose (49%) and has a lower oxygen content. It appears to be degraded by Hymenomycetes and Gasteromycetes (Hudson, 1968). According to Hurst and Burges (1967) conifer lignin, which contains vanillin, is a phenyl propane polymer and is degraded by extracellular enzymes in several stages which are not yet worked out. In *Pinus strobus* litter, lignin, as measured by its methoxyl content, was constant over the first 165-day period of acid hydrolysis but decreased slightly from 165–1200 days (Sowden and Ivarson, 1962). Lignin, therefore, tends to accumulate in the lower layers of the litter as lignin–protein complexes, thus contributing considerably to the formation of humus (Shewan, 1936; Waksman, 1952). Shewan showed that these complexes increased continuously down the profile of a soil under *Pinus sylvestris*.

Carbon dioxide evolution has been used frequently as a measure of biological activity in the litter. The amount of CO_2 evolved measures the gross breakdown less the amount of carbon incorporated into the tissues of soil organisms. Kornev (1962), working in *Pinus* plantations, found that the evolution of CO_2 decreased lower down in the litter and suggested that this decrease was related to the unilateral consumption by micro-organisms of available organic matter in the upper layers, with the consequent accumulation of unavailable compounds. The evolution of CO_2 varied with the season, increasing through the summer to a maximum in August with a second peak in October following needle fall.

Hayes (1965a) in his studies of the decay of surface litter from three coniferous species found an increase in carbon content on a dry-weight basis over the first 16 months of decomposition, suggesting that substances which contained relatively little carbon in their molecular structure were being lost preferentially. These could include sugars, hemicelluloses, pectins and organic acids. The loss of these carbohydrates led to a rapid decrease in the C:N ratio in the first few months of decomposition.

Most of the nitrogen reaching the forest floor comes in the leaf litter and the amount will vary with the species and age of the crop and the condition of the site. Figures of 8–55 kg ha^{-1} years are quoted for coniferous forests by Miller (1966), who pointed out that additional nitrogen is available through rainfall and root excretion. Rodin and Bazilevich (1967) give an even wider range of 13–116 kg ha^{-1} year. Thus nitrogen is present in soils under conifers in large amounts but, in contrast to mull soils, a high proportion is usually unavailable for plant growth.

In a survey of soils in the U.S.S.R., podsolic forest soils contained from 100 to 300 t of humus and from 6 to 14 t of nitrogen per hectare in the top metre and the C:N ratio varied from 8·7 to 12·0 (Vilenskii, 1957).

Miller (1966) in a detailed analysis of a 36-year-old stand of Corsican pine on a sandy site in Scotland found nearly 2 t of nitrogen on the forest floor in 200 t of organic matter.

During decomposition, some protein nitrogen is mineralized by the soil microflora, with the release of carbon dioxide and ammonia, whilst the remaining nitrogen is incorporated into microbial tissue such as chitin, or fixed during humification by the formation, for example, of lignin protein complexes. Several workers have noted the slow rate of loss of nitrogen from coniferous litter. Voigt (1965) found that he could recover 60–90% of the original nitrogen from decompositing litter of *Tsuga heterophylla* (Ref.) Sarg., *Thuja plicata* D. Don, *Pinus resinosa* Ait. and *Pseudotsuga menziesii* after 15 months in laboratory experiments. Ivarson and Sowden (1959) also found only small losses of nitrogen from litter and soils under *Pinus strobus* over a 6-month period although the number of fungi and the production of carbon dioxide both increased, and Hayes (1965*a*) obtained similar results with litter from three conifers in Wales. Tamm and Pettersson (1969) in similar experiments, incubated humus from the L layer in *Pinus sylvestris* and *Picea abies* stands for two years in aerobic conditions at room temperature. This resulted in up to 25% of the total nitrogen being mineralized and released, mainly as ammonia. According to Sowden and Ivarson (1959) the amino-acid composition of *Pinus strobus* litter does not change appreciably during the early stages of decomposition.

Active ammonification of protein nitrogen takes place in the F_1 layer through the action of the microflora (Guittet, 1967) and nitrification occurs in small pockets of high pH at microsites in the F_2 and H layers. At these sites there is considerable Actinomycete (Kaila, 1954; Williams and Mayfield, 1971) and urease activity (Kornev, 1962).

Total release of nitrogen from the litter is prevented by the process of humification which may be thought of as starting in the leaf. Polyphenols are at a maximum in fresh growing leaves and reduce in quantity as the leaves senesce, die, fall and decay (Coulson *et al.*, 1960). The protein polyphenol complexes, formed before leaf fall, are very resistant to microbial degradation, and mesophyll cells have been shown to be an important constituent of humus (Handley, 1954). In the view of Coulson *et al.* (1960) the great majority of reducing compounds found in the litter are polyphenolic complexes. The protein part of the complex is probably decomposed by bacteria by ring fission of the quinone groups.

The several theories of humification are summarized by Felbeck (1971). Whether humification is through direct alteration of plant material such as lignin, through cell autolysis or through microbial synthesis, the net result is an ill-defined association of carbohydrates, lignin, amino acids, amino sugars, phenolic compounds and other organic substances. The

humus complexes contain humin, humic acid and fulvic acid. The total amount of humic acid in the top 100 cm of a *Pinus* stand was estimated by Zonn and Sokolov (1960) to be about 150 t ha^{-1} with about two-thirds fulvic and one-third humic acid, and these figures accord well with those given by Vilenskii (1957) for Russian soils in general.

The first stage of the decomposition of these very resistant substances is probably by a reduction of the carboxylic groups to primary alcohol groups (Felbeck, 1971). Burges and Latter (1960) have demonstrated that a number of fungi, including species of *Polystictus*, *Trametes*, *Hypholoma* and *Polyporus*, are capable of decomposing humic acid. In soils under conifers the degradation product of humic acid is usually a flavenoid (Hurst *et al.*, 1962).

Webley and Jones (1971) have drawn attention to the inadequacy of our present state of knowledge of the chemistry of many soil organisms and in particular to the dearth of information on their biological transformations in soil. Chitin, a constituent of both fungal cell walls and meiofaunal exoskeletons, can be broken down by fungi, Actinomycetes and bacteria (Goodfellow *et al.*, 1968; Veldkamp, 1955). The ammonia released from chitin decomposition is utilized by Streptomycetes, usually at microsites of ammonia absorption on organic fragments (Williams and Mayfield, 1971). The degradation of remains of the microflora is not known specifically for coniferous litter. In general, bacteria may be lysed by other bacteria, phages, Actinomycetes or fungi. Fungi can be lysed by bacteria, those fungi with pigmented hyphae being more resistant than non-pigmented forms.

VII. Rate of Decomposition

The rate of decomposition of mor litter is slow in comparison with mull litter. This is due primarily to a combination of a low-base status substrate containing resistant substances such as waxes, resins and lignin and the cold climate characteristic of the boreal forests. Such conditions do not encourage an active microflora or meiofauna.

The amount of litter in each layer will depend upon the time and amount of needle fall and the rate of decomposition. Kornev (1962) found about 8 t ha^{-1} air-dried litter in the L layer and 13 t ha^{-1} in the F layer in a variety of *Pinus sylvestris* associations in Russia, and Guittet (1967) found about 7 t ha^{-1} in the L and 23 t ha^{-1} in the F layers of a 45-year-old stand of the same species in France. In another study of *Pinus sylvestris* made by Kendrick (1959) the oven-dry weight of needles was 1·7 t ha^{-1} in the L and 22 t ha^{-1} in the F layers, although the total annual needle fall was 4 t ha^{-1}. From his results, Kendrick deduced that a needle was in the L layer for about 6 months, in the F layer for 2 years and in the F_2 layer for

7·5 years. Guittet (1967) made a similar estimate for the rate of decomposition of *Pinus* litter in France, the time to reach the humus layer being approximately 10 years, with a further 10 years in the humus layer. In the case of *Picea abies*, Meyer (1962) estimated that between 17 and 31 years were needed for total mineralization.

The loss in dry weight during decay has been estimated by various workers under a variety of conditions. Mikola (1954) estimated a loss of between 11 and 30% in the first year and 25–48% in the second year in litter of *Pinus sylvestris*, *Picea abies* and *Larix* sp. in the forest, most of the loss being attributable to cellulose decomposition. Hayes (1965a), working in laboratory conditions with *Picea sitchensis* and *Abies grandis*, noted decreases of 20–30% in the first two months and 50% in 16 months of incubation. Loss in dry weight was 24% after 2 years and 47% after 7 years in the stand of *Pinus sylvestris* examined by Kendrick (1959). In New Zealand, litter of *Pinus radiata* showed a progressive decrease in dry weight over 3–4 years and soil animals became more important in the decomposition process after about 3 years (Will, 1968).

It has been stated already that coniferous leaf litter is more resistant to decomposition than is broad-leaved litter. Daubenmire and Prusso (1963) showed that considerable variation in resistance to decay exists between the litters from 11 conifer species. *Pseudotsuga* decomposed readily relative to *Picea* and *Tsuga* at 10°C in the laboratory. However, these authors pointed out that the rating of litters according to their decomposition in an artificial environment depends very much upon the temperature chosen for the test. They suggested that needle anatomy, together with the nutrient status of the needles and the possible production of substances toxic to microorganisms, might control the rate of decomposition.

Factors of the environment such as temperature and moisture are probably most important in governing the rate of litter decomposition (see Gray and Williams, Chapter 19). Mikola (1960) found that in Finland the rate of decomposition of litter of *Pinus sylvestris* and *Picea abies* increased with increase in the mean summer temperature or the temperature of the growing season. In southern Finland (60°20'N) the rate averaged about 40% faster than in Lapland (68°2'N). Similarly, in Japan under various conifers in different regions the rate of litter decomposition was related directly to an index of the variation of average annual temperatures above 5°C (Shidei and Tsutsumi, 1962).

Soil moisture affects the rate of decomposition since excess moisture leads to lack of aeration and a reduction in microbial activity (Mikola, 1954; Witkamp, 1966). It has been noted already that soil moisture and temperature control the movement and feeding activity of mites (Hayes, 1965*c*; Usher, 1971; Metz, 1971) and springtails (Usher, 1970). Leaching *Pinus*

echinata litter with water increased decomposition under laboratory conditions (Kowal, 1969).

Witkamp (1966) has noted that microbial activity tends to be related inversely to the C:N ratio so that, in coniferous litter, activity increases with increase in depth. He found, using a serial dilution-plate method, that loss in weight of decomposing needles of *Pinus taeda* was correlated highly with microbial population estimates. The annual input of nutrients to the litter of *Pinus jeffreyi* in the pollen rain has been shown by Stark (1972) to stimulate activity of the microflora in the F layer. The pollen is colonized by fungi with a subsequent release of nitrogen and phosphorus to the benefit of the tree crop.

From a silvicultural point of view, to aid litter decomposition, an admixture of broad-leaved species with conifers together with thinning conditions which promote the development of an herbaceous ground flora are to be recommended (Mikola, 1954). Florence (1965) has suggested that the addition of litter of *Lithocarpus densiflorus* (Hook and Arn.) Rehd. (tan oak) might stimulate microbial activity in *Sequoia sempervirens* (Lamb.) Endl. forests in western North America.

An alternative means of stimulating microbial activity is by artificial fertilization. Although not much work has been done on this subject in relation to microbial populations, it appears that the addition of nitrogen in the form of urea can stimulate microbial activity in litter of *Picea mariana* (Roberge and Knowles, 1966). Williams (1972) showed that a variety of fertilizer treatments failed to give a lasting change in the chemical composition of humus under *Pinus sylvestris* in Scotland. Only urea produced a significant increase in total nitrogen but the addition of calcium stimulated microbial activity in the humus layer.

VII. Discussion—Present State of Research

This account serves to show that, although quite a lot is known about the general structure and chemistry of needles, the pattern and amount of needle fall and the microflora and meiofauna involved in needle decomposition, relatively little is known of the detailed physical and chemical changes and microbial successions occurring during this process.

There is a dearth of information not only on the specific action of individual fungi but also on the interactions between these fungi. We need to know which fungi are acting where and to what effect. To this end studies of tissue disintegration using a histochemical approach might be applied not only to needles in the litter but also to those still on the tree so that the condition of needles entering the litter might be better described.

There is general agreement that animals accelerate the action of the

microflora in decomposition. Macfadyen (1961) has summarized the general catalytic action of the meiofauna in soils. In coniferous litter the Acarina and Collembola, although inefficient feeders, almost certainly accelerate decomposition by comminution of the litter and by transporting fungal spores to new sites. However, we know very little of the precise relationship of fungi to the meiofauna, of the palatability of different fungi and needle tissues to Acarina and Collembola, and of the factors governing the rate of feeding of these animals in the litter. The use of radiotracers should prove a useful tool to help our understanding of these complex litter systems (Crossley, 1970).

In relation to nutrient mineralization and cycling, Stark (1972) has pointed out that we have little idea of the significance of fungi in retaining or releasing elements in the litter or of the mechanisms of concentration and release. In particular the role of bacteria and Actinomycetes in mineralization requires further elucidation. Studies on mineralization, humification and humus decomposition are notoriously difficult and we must await the development of improved techniques in this field to help us in our understanding of the processes of mull and mor formation.

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